The history of Aplomado Falcon Falco femoralis subspecies diagnoses

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The history of Aplomado Falcon *Falco femoralis* subspecies diagnoses

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Summary.—I present the historical details associated with early 20th century descriptions of Aplomado Falcon subspecies. I identify potential weaknesses in these diagnoses that justify re-examination of traditional taxonomy, and stress that climate change, habitat modification and large-scale reintroduction efforts may have altered or eliminated any valid subspecies boundaries that once existed. I recommend that conservation efforts in the Northern Hemisphere focus on the Chihuahuan Desert of Mexico where Aplomado Falcons have declined severely in recent years.

In North America in the late 19th century, acceptance of subspecies as valid taxonomic units led to proliferation of numerous trinomials. This process accelerated in the first half of the 20th century (Coues 1871, Stejneger 1884, Stresemann 1975, Haffer 1992, Barrow 1998). By 1945 the number of named avian subspecies had exceeded 28,500, with new trinomials being coined at a rate of *c*.200 per year (Mayr 1946). In part, this trend reflected awareness that species are not fixed entities but demonstrate geographic variability potentially indicative of ongoing speciation (Ridgway 1879). New subspecies resulted partly from demotion of closely related, similar-looking species, but also from subdivision of single species into separate geographic forms (Stejneger 1884, Haffer 1992, Barrow 1998). Disruption of the Linnaean binomial system, the lumping of many formerly separate species, the trivial nature of diagnostic characters, and the resulting instability of nomenclature generated abundant criticism on both sides of the Atlantic (Coues 1884, Sharpe 1896, Allen 1890, Clark 1902, Sclater 1904, Ridgway 1923). In 1886, the American Ornithologists' Union (AOU) proposed restricting subspecies designations to geographic forms interconnected by intergradation within contiguous geographic distributions (AOU 1886).

Further proliferation of new subspecies led to demands for more consistent and less subjective criteria. Clark (1904), for example, proposed that size differences of less than 5% should not provide the basis for a subspecies diagnosis. He also urged that diagnostic characters be sufficiently conspicuous to be translatable into 'intelligible language or figures'. Allen (1905) and Merriam (1919) opposed such restrictions. Subsequently, Grinnell (1921) and Ridgway (1923) urged that proof of intergradation be revived in the interest of slowing further changes to nomenclature. But Chapman (1924), like Allen, objected to any 'unreasoning adherence to a purely arbitrary man-made law'. Swarth (1931) agreed, stating that 'science is not a game, to be won or lost according to set rules'. At another extreme, Hartert (1910) and Huxley (1939) proposed limiting subspecies designations to isolated (at least ecologically) and distinctive subpopulations, thereby making such diagnoses inappropriate for geographic forms interconnected by more gradual or 'clinal' variation (Huxley 1939). Nevertheless, taxonomists persisted in basing diagnoses on extremely small sample sizes of measured specimens, subjective

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assessments of plumage differences, and inaccurate knowledge of the location of breeding vs. wintering distributions (Mayr 1935, Parkes 1982, Wilson & Brown 1953). Due to these and many other concerns, Mayr (1951) decried the waste of time spent by taxonomists 'describing and naming trifling subspecies'. Wilson & Brown (1953) called the system 'illusory and superfluous' and hoped it would eventually be relegated to 'nomenclatural limbo'.

Although controversy regarding subspecies has continued beyond the 20th century it still basically revolves around the concept's utility, its definition, and how best to evaluate putative races (Haig *et al*. 2006, Patten 2010, Winker 2010, McCormack & Maley 2015, Patten & Remsen 2017). Despite these concerns, the AOU has consistently emphasised that subspecies have value in demarcating unique coloration and morphology associated with specific geographic regions, migratory routes, habitats and behaviours; and to study the early stages of speciation (AOU 1886, 1983, 1998). Subspecies can also play a critical role in conservation biology if they identify evolutionarily unique populations and facilitate efforts to preserve the evolutionary potential of declining species (Haig *et al*. 2006, Phillimore & Owens 2006, Haig & D'elia 2010). In this regard, 79 subspecies currently appear on international lists of avian taxa designated Endangered or Threatened under the US Endangered Species Act of 1973 (as amended, 16 U.S.C. 1531 *et seq*.). Complicating such listings is the possibility that many subspecies, especially those described in the late 19th and early 20th centuries, may be invalid based on modern morphometric, colorimetric and genetic standards (Zink 2004, Dickinson & Remsen 2013, Patten & Remsen 2017, and others). Dickinson & Remsen (2013) cautioned that current global checklists may still recognise 'hundreds' of invalid subspecies. This possibility has spurred ongoing efforts to re-evaluate 'older' subspecies (Dickinson & Remsen 2013, Gill & Donsker 2019). Because of the risk of misallocating conservation resources, subspecies currently listed as threatened or endangered perhaps deserve highest priority in this endeavour (Crandall *et al*. 2000, Zink 2004, Fitzpatrick 2010, Patten 2010).

A potential case in point is provided by the Aplomado Falcon *Falco femoralis*, a widespread Neotropical raptor, well known to ornithologists since at least the early 19th century. By the early 20th century it was known to breed in Panama and various parts of South America but also in the south-west USA and north-east Mexico (Salvin & Godman 1904). Some authorities interpreted the lack of specimens from most of Mexico and northern Central America as a significant gap in the breeding range (Salvin & Godman 1904, Griscom 1932). This, plus one other supposed 'gap' in Argentina and perceived differences in size and coloration, served to justify subdividing the species into three, sometimes four, subspecies (Todd 1916, Swann 1922, Chapman 1925). Although Aplomado Falcon is considered Not Threatened or Least Concern (Bildstein *et al*. 1998, BirdLife International 2018, CITES 2018), in 1986 the northern subspecies so-called 'Northern Aplomado Falcon' *F. f. septentrionalis*, was listed as 'Endangered' under the US Endangered Species Act (Shull 1986, Keddy-Hector 1990). This rested on evidence of extensive pesticide contamination in eggs of eastern and southern Mexican Aplomado Falcons, as well as equivocal evidence of population declines in the south-west USA in the early 20th century (Kiff *et al*. 1980, Hector 1987, Keddy-Hector 2000). At no time during preparation (by this author) of materials to justify the Endangered status was the validity of the northern subspecies questioned. Here, I attempt to rectify this deficiency by providing a historical analysis of the evidence used to designate this and the other subspecies of this charismatic falcon.

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TABLE 1

Averages, minima and maxima of wing chord measurements (mm) of Aplomado Falcon *Falco femoralis* subspecies as presented by different authorities (sample sizes in parentheses).

Subspecies	Male	Female	Reference
INITIAL DIAGNOSES			
F. f. septentrionalis			
Arizona (2)	267 (1)	294 (1)	Todd (1916)[a],
Arizona, Texas, Tamaulipas (10)	259 (6) 253–263	289 (4) 283–294	Todd & Carriker (1922)[a,b]
F. f. femoralis			
Colombia, Bolivia, Argentina (12)	240 (6) 230–248	267 (6) 263–271	Todd & Carriker (1922)
F. f. pichinchae			
Ecuador (3)	--	290–295	Chapman (1922)[a]
FIELD MUSEUM SPECIMENS			
F. f. septentrionalis			
Texas, Tamaulipas, Nicaragua (11)	255–260	270–304	Hellmayr & Conover (1949)[c]
Not specified (15)	257 (8) 248–267	290 (7) 272–302	Blake (1977)[c]
F. f. femoralis			
Argentina, Bolivia, Brazil, Guyana, Panama, Paraguay, Uruguay, Venezuela (22)	225–252	255–290	Hellmayr & Conover (1949)[c]
Not specified (48)	237 (23) 226–254	263 (25) 245–282	Blake (1977)
F. f. pichinchae			
Argentina, Bolivia, Colombia, Chile, Peru (13)	256–278	267–313	Hellmayr & Conover (1949)[c]
Not specified (15)	258 (5) 235–272	298 (10) 290–311	Blake (1977)
COMPOSITE SAMPLES			
F. f. septentrionalis			
Arizona, Texas, Chihuahua, Coahuila, Tamaulipas, Veracruz, Tabasco, Campeche, Chiapas (70)	262 (38) 229–289	293 (32) 267–314	DPK-H unpubl.[a,b,c,d,e,f]
F. f. femoralis			
Argentina, Belize, Bolivia, Brazil, Colombia, Guyana, Nicaragua, Paraguay (53)	238 (34) 220–260	269 (19) 254–285	DPK-H (unpubl.)
Argentina (28)	257 (9) 247–275	280 (19) 266–288	Liébana (2015)[d]
F. f. pichinchae			
Bolivia, Chile, Peru (19)	268 (11) 256–280	301 (8) 286–318	DPK-H (unpubl.)

Sources: [a] US National Museum, Washington DC (USNM); [b] Carnegie Museum, Pittsburgh (CM); [c] Field Museum of Natural History, Chicago (FMNH); [d] Trapped, wild adults (Montoya 1995); [e] Museum of Comparative Zoology, Cambridge, MA (MCZ); [f] First-generation breeding project birds taken from nests and measured as adults at Peregrine Fund's Univ. of California Santa Cruz facility.

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History

In 1916, W. E. Clyde Todd, of the Carnegie Museum, proposed that Aplomado Falcons collected in Arizona represented a subspecies that he named *F. fusco-coerulescens*[1] *septentrionalis*. Todd described this form simply as 'similar in color to *F. fusc. fusco-coerulescens*, but decidedly larger' (Fig. 1). He provided no additional details, discussion of the geographic distribution, or any analysis of size differences. In fact, the account contains measurements of only two specimens, both from the same nesting territory near Fort Huachuca in south-east Arizona (Bendire 1887). These details appear at the end of a four-part series containing similarly brief 'diagnoses' of 55 new subspecies, 25 new species and one new genus along with a promise that more details would be forthcoming (Todd 1912, 1913, 1915, 1916).

Six years later, Todd fulfilled his promise by providing measurements of 11 North American (Arizona, Texas, and Tamaulipas) and ten South American (Argentina, Bolivia, Colombia) specimens (Todd & Carriker 1922). The wing chords of the two groups do not overlap and the North American sample averages 8% larger than that from South America (Table 1). Just one comment concerning plumage appears, in reference to the dark abdominal band of the northern birds: 'the black area on the lower parts more extensive'. But Alexander Wetmore (1926) of the Smithsonian considered that plumages of birds in the two regions were 'identical', as did John Cassin in his characterisation of the first US specimen: 'precisely identical with the South American bird' (Cassin 1855). Swann (1936) mostly agreed: 'scarcely differs in plumage from the southern typical form . . . slate of upper parts with a brownish shade' but added 'tail more widely banded with white'. Hellmayr & Conover (1949), after reviewing the large series of Aplomado skins at the Field Museum of Natural History, Chicago, supported and augmented Todd's description: 'Differs from the South American races by its light grayish upper parts (this being especially noticeable on the crown), extensive and solid black pectoral zone, and the light tone of the zinc-orange abdominal area'. Wetmore (1965) ultimately agreed: 'distinguished by lighter-gray upper surface, with the breast solid black, and somewhat larger size'. Emmet Blake's characterisation, also based on Field Museum specimens, is essentially identical and emphasises the larger size, complete abdominal band, and 'paler, more grayish upper surface' (Blake 1977). Like Hellmayr & Conover, Blake also mentioned the relative paleness of the lower abdomen 'and tibiae'.

In 1925, Frank Chapman of the American Museum of Natural History, New York, described *F. fusc. pichinchae*, based on the larger size of three females collected in the Andes of Ecuador (Chapman 1925). Wing chords of these specimens were as large as those of the largest North American birds (Table 1). Chapman also described the black area of the abdomen and flanks of Ecuadorian specimens as 'smaller and divided medianly'. Swann (1936) later copied and extended Chapman's description: 'darker above, especially on the crown; zinc orange tints averaging deeper on the breast, the black area smaller and divided medianly' and called this the 'Andine Aplomado Falcon'. Hellmayr & Conover (1949) reiterated that *F. fusc. pichinchae* is 'considerably darker throughout, upper parts duskier, the pileum especially so; the ochraceous abdominal area deeper in tone; the black pectoral zone less extensive and more or less broken medially'. Blake (1977) once again agreed with

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[1] Vieillot (1817) derived *Falco fusco-coerulescens* from Azara's (1802) description of '*obscuro azulejo*', one of the smaller Neotropical falcons ('*los alconcillos*'). This name had priority until Peters & Griswold (1943) pointed out that Azara's description of *obscuro azulejo* better fit the smaller Bat Falcon *F. rufigularis*. Priority then shifted to Temminck's (1822) *F. femoralis* ('*Faucon a culotte rousse*') that he based on actual specimens and Azara's species description of an *alconcillo* that he called the '*aplomado*'.

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Figure 1. Female and male specimens of Aplomado Falcon subspecies, from left to right: *F. f. septentrionalis*, *F. f. femoralis* and *F. f. pichinchae* (© Field Museum of Natural History, Chicago)

Hellmayr & Conover and emphasised the larger size (than the nominate form), incomplete abdominal band, and darker, more intense coloration.

A footnote in Griscom (1932) referred to a fourth subspecies. This acknowledged Swann's (1922) split of South American Aplomado Falcons east of the Andes into northern and southern forms. Swann (1922, 1936) credited Vieillot (1817) with describing the nominate form that Swann called the Southern Aplomado Falcon *Rhynchofalco*[2] *fusc. fusc*. and Temminck (1822) with describing the Lesser Aplomado Falco *R. fusc. femoralis*. In Swann's view, Southern Aplomado Falcon was a larger, migratory form in Argentina and Chile, whereas Lesser Aplomado Falcon was a smaller, non-migratory form inhabiting the rest of South America east of the Andes. He distinguished the latter as 'more bluish slate, less brownish' (than *R. fusc. fusc*.), with the tail having 'much less white in it'. Wetmore (1939) opposed this and stated that Swann's Southern Aplomado Falcon was invalid because typical Lesser Aplomado Falcons had been collected at the type locality of the Southern Aplomado Falcon. He also felt that 'The geographic races of this falcon are not clearly outlined at the present time'. Peters & Griswold (1943) rejected Swann's Southern Aplomado but stated that Aplomado specimens from 'Chile and southern and western Argentina' were larger than typical *F. f. femoralis*. Hellmayr & Conover (1949) did the same, but suggested that the nominate form 'might have to be subdivided, as suggested by Swann', apparently because specimens from southern Argentina (Chubut) were almost as large as typical *F. f. pichinchae* and possessed a 'medially broken blackish pectoral zone',

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[2] *Rhynchofalco* is a monotypic genus or subgenus name proposed for Aplomado Falcon by Ridgway (1873) that reflected his belief that *F. femoralis* was not that closely related to Bat Falcon and Orange-breasted Falcon *F. deiroleucus*, which he and others placed in genus *Hypotriorchis*.

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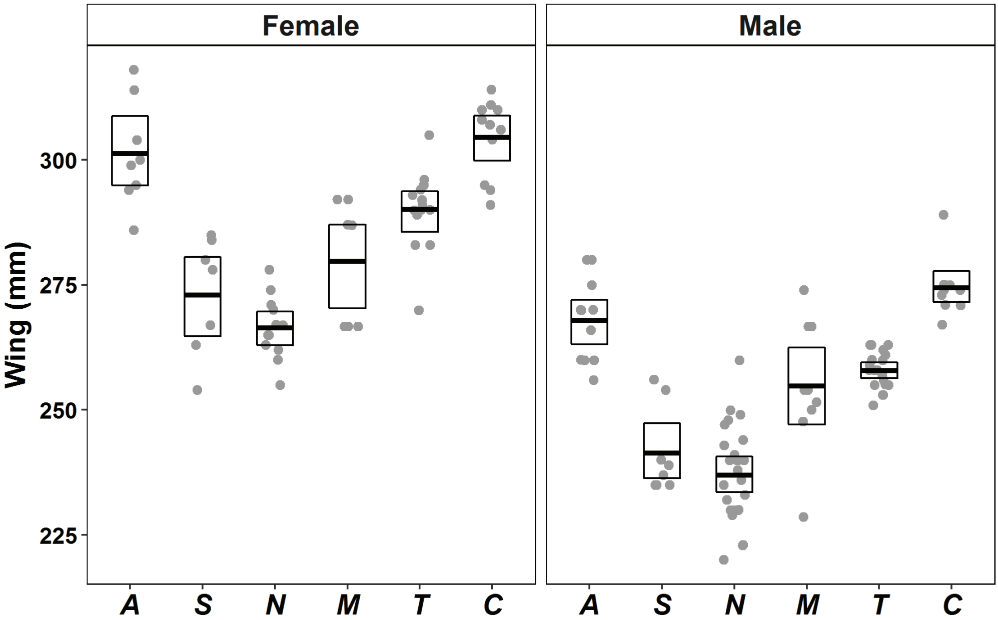

Figure 2. Comparison of means and bootstrapped 95% confidence limits of wing chord measurements (uncorrected for shrinkage) of Aplomado Falcon *F. femoralis* regional groups arranged to show variation in size along gradients of elevation and latitude: 'A' = *F. f. pichinchae* from the Andes of Chile, Ecuador, Peru and western Bolivia; 'S' = *F. f. femoralis* from southern South America, in Argentina and Paraguay; 'N' = *F. f. femoralis* from Central America and northern South America east of the Andes and north of Argentina and Paraguay; 'M' = *F. f. septentrionalis* from the tropical coastal plains of Mexico; 'T' = *F. f. septentrionalis* from the coastal plain of north-east Mexico and southern Texas; and 'C' = *F. f. septentrionalis* from the Chihuahuan Desert of Arizona, Chihuahua and Coahuila.

while also being, like *F. f. septentrionalis*, 'very light and gray above'. This, however, partially conflicted with Peters & Griswold (1943) who described specimens from this region as 'browner and darker' than typical *F. f. septentrionalis*.

Complicating all of this was the assumption that Aplomado Falcons were highly migratory (Swann 1922, Bent 1938, Wetmore 1939, Hellmayr & Conover 1949, Brown & Amadon 1968, Blake 1977). Swann (1922) and Wetmore (1939), for example, stated that the larger Aplomado Falcons of Peru were actually wintering *F. f. septentrionalis* from the USA and Mexico. Wetmore (1939) even suggested that Swann's larger, paler Southern Aplomado might be wintering *F. f. septentrionalis*. This view obviously conflicted with Swann's (1922) belief that Southern Aplomado Falcons migrated north in winter and partly explains Wetmore's reticence as to the validity of Southern Aplomado Falcon. But Hellmayr & Conover (1949) accepted Swann's scenario as an explanation for the mixture of smaller darker, and larger paler Aplomado specimens in east-central Argentina (Buenos Aires province). They proposed that this region was not inhabited by breeders, but only by 'migratory visitors, the small dark-backed ones coming from the north [*F. fusc. femoralis*?], the larger, paler ones being wanderers from Patagonia'. Eggs (Western Foundation of Vertebrate Zoology, Camarillo, and National Museum of Natural History, Washington DC) and field studies, however, show that the species does breed in Buenos Aires and surrounding provinces (Bó 1996, De Lucca & Saggese 1996, De Lucca & Quaglia 2012, De Lucca *et al*. 2013, Salvador 2013, Liébana 2015, De Lucca & De Lucca 2017). Residents from this population are also larger than typical *F. f. femoralis* (Liébana 2015; Table 1).

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In the Northern Hemisphere, the paucity of specimens from Middle America coupled with disproportionate collecting in the south-west USA (Keddy-Hector 2000, Keddy-Hector *et al*. 2017) created the impression that more than 2,000 km separated Aplomado Falcons breeding in Arizona, New Mexico, Texas and Tamaulipas from the nearest resident population in western Panama. This notion appears to have supplanted an initial supposition that the species was resident throughout most of Mexico and Central America (Baird *et al*. 1874). Salvin & Godman (1904), for example, stated 'though not infrequent in Mexico, it is probably only a winter visitor there'. Griscom (1932) described the geographic distribution as 'remarkably disconnected' and thought that Aplomado Falcons of the south-west USA must winter in Guatemala. He also considered western Panama (Agua Dulce) the northernmost occurrence of resident *F. f. femoralis*. Perhaps reinforcing this belief was the possibility that many (perhaps most) US specimens—those collected by Frank Armstrong at 'Ft. Brown', 'Brownsville' or 'Cameron Co.', Texas—actually came from Mexico (Strecker 1912, Oberholser 1974, Hector 1987, Keddy-Hector 2000, Keddy-Hector *et al*. 2017).

One effect of this 'disconnection' was to make the known breeding range easily meet the liberating suggestion of Merriam (1897, 1919) and Stone (1903) that subspecies designations, in the absence of proof of intergradation, be applicable to isolated populations even if they differed only slightly from nearest neighbouring populations. This also met Huxley's (1939) criterion that a valid subspecies be 'partially or wholly isolated from related groups'. But the gap in the breeding range steadily shrank as collectors supplied specimens from additional parts of Middle America. This was acknowledged by Friedmann *et al*. (1950) who described the Aplomado as resident from the south-west USA south to the Yucatán and possibly even to Guatemala. This view has been confirmed by specimen and sight records from the tropical lowlands of San Luís Potosi, Veracruz, Tabasco, Campeche and Chiapas (Kiff *et al*. 1980, Hector 1981, reviewed by Keddy-Hector 2000, Keddy-Hector *et al*. 2017). Binford (1989) allowed for the possibility that the species was resident in Oaxaca, but felt that his February records only indicated winter residency. He was apparently unaware that, at least on the Caribbean slope, the species has an extended breeding season and resident pairs can commence incubation before the end of February (Keddy-Hector 2000). Howell & Webb (1995) suggested the species also breeds in Guerrero. Hellmayr & Conover (1949) postulated incorrectly that an adult male collected in early August in Nayarit (San Blas) indicated nesting. Breeding has also been documented in Chihuahua and Coahuila, but apparently from nowhere else in the Mexican altiplano or western Mexico (Hector 1981, Montoya 1995, Macías-Duarte 2002, Keddy-Hector *et al*. 2017).

Evidence of nesting also began to appear in Central America north of Panama. For Belize, Russell (1964) listed breeding-season records in February–June. In Nicaragua, Howell (1972) collected breeding-season (February–March) specimens including a presumed pair, of which the female had enlarged ovaries. Both authorities assigned specimens from the Caribbean slope to *F. f. femoralis*. Howell also noted that two immatures collected in April 1904 on the Pacific slope were intermediate in size between *F. f. septentrionalis* and *F. f. femoralis*. Hellmayr & Conover (1949) assigned these immatures to *F. f. septentrionalis* and interpreted them as migrants from the north, the month of collection, however, hints at a local natal site, and suggests the existence of a zone of intergradation connecting the two subspecies along the Pacific slope. A similar pattern occurs on the Caribbean slope, with southern Mexican *F. f. septentrionalis* averaging only slightly larger than *F. f. femoralis* from Central America and northern South America, but smaller than *F. f. septentrionalis* of the Chihuahuan Desert of Arizona, Chihuahua and Coahuila (Fig. 2). The species has also been observed and is probably resident in El Salvador (Jones & Komar 2006), Guatemala (Eisermann & Avendaño 2018) and Honduras (Marcus 1983). Aplomado Falcons were first

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reported from Costa Rica in 1980, and there have been more recent sight records, mostly of subadults suggesting these are either vagrants or the product of local resident pairs (Koford *et al*. 1980, Jones & Komar 2011, eBird 2018).

The existence of non-breeding season specimen and sight records at higher latitudes and higher elevations has weakened the notion that this falcon is highly migratory (GBIF2018, eBird 2018). Bildstein (2004, 2006), in fact, classified it as a 'partial migrant' or 'altitudinal migrant'. Keddy-Hector *et al*. (2017) recommended changing this to 'local migrant'. This view is supported to some degree because this species clearly satisfies Bergmann's Rule (Bergmann 1847), with larger falcons inhabiting higher latitudes or higher elevations (Keddy-Hector *et al*. 2017). Rensch (1936), Mayr & Vaurie (1948), Mayr (1956), Zink & Remsen (1986) and Olson *et al*. (2009) suggested that highly migratory species tend not to show this pattern. Ashton (2002) found that 86% of sedentary and 67% of migratory species follow Bergmann's Rule. But Ferguson-Lees & Christie (2001) mentioned partial migration north from Patagonia and also some movement of Peruvian Aplomado Falcons from the high Andes to coastal locations. Sick (1993) described 'small migrant flocks' in August in southern Brazil. Macías-Duarte (2018) has recently documented 300 km dispersal by fledglings from Chihuahuan nests.

Closure of the gap in breeding distribution also narrowed the gap (and increased the overlap) in size between putative northern and nominate forms (Table 1, Fig. 2). Some of this is simply the result of increasing variability as a function of sample size, but enhancing this effect was larger numbers of specimens from coastal localities and tropical latitudes where Aplomado Falcons tend to be smaller. In this respect, wing chords of higher elevation Chihuahuan Desert Aplomado Falcons (Montoya 1995) averaged 7.0–8.5% (male–female) larger than those of southern Mexican (Campeche, Chiapas, Tabasco and Veracruz) birds (DPK-H unpubl.; Fig. 2). Wing chords of southern Mexican falcons averaged 6.2–3.2% (male–female) larger than those of *F. f. femoralis* specimens from Central America and northern South America.

Discussion and Conclusion

Despite the larger size and allegedly paler coloration of Aplomado Falcons of southern Argentina, most modern authorities recognise only *F. f. femoralis*, *F. f. septentrionalis* and *F. f. pichinchae* (Blake 1977, Mayr & Cottrell 1979, Dickinson & Remsen 2013, Keddy-Hector *et al*. 2017). In comparing these forms, Hellmayr & Conover (1949), Friedmann (1950), Wetmore (1965) and Blake (1977) generally agree on the following characters (Tables 2–3): (1) *F. f. septentrionalis* and *F. f. pichinchae* both larger than *F. f. femoralis*; (2) *F. f. pichinchae* incomplete dark abdominal band; (3) *F. f. pichinchae* darker and more deeply coloured; and (4) *F. f. septentrionalis* more greyish dorsally. Only Swann (1936) mentioned broader white tail-bands in *F. f. septentrionalis*. Disagreements probably stemmed from the subjective and constraining process of using single colour categories to generalise variable and subtle differences typically present in whichever series of skins a taxonomist examined. Variable degrees of fading of older specimens, and of the colours of live birds prior to their collection, further complicated assessments, as did confusion as to differences between the more brownish subadult and more bluish or greyish adult dorsal colour. The last factor possibly explains the description of two Panamanian (Veraguas) *F. f. femoralis* as 'dark brown above' (Hellmayr & Conover 1949); Swann's (1936) application of 'brownish' to *F. f. septentrionalis*; and Peters & Griswold's (1943) 'browner and darker' southern South American Aplomado Falcons. Together these inevitably led to seemingly contradictory characterisations such as Blake's (1977) description of *F. f. septentrionalis* as 'paler, more grayish' than *F. f. femoralis*, and *F. f. femoralis* as 'less bluish gray' than *F. f. septentrionalis*; in the aftermath of Swann's

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TABLE 2

Comparison of diagnostic characters of three Aplomado Falcon *Falco femoralis* subspecies.

	F. f. septentrionalis	***F. f. femoralis***	***F. f. pichinchae***
Body size	Larger	Smaller	Larger
Coloration	Paler, more greyish	Darker to paler and more greyish	Darker
Abdominal band	Complete	Complete	Incomplete
White tail-bands	Broader	Narrower	Narrower

TABLE 3

Comparison of diagnostic characters of Aplomado Falcon *Falco femoralis* subspecies, with *F. f. femoralis* subdivided into Swann's (1936) Lesser and Southern Aplomado Falcons.

	F. f. septentrionalis	***F. f. femoralis***		***F. f. pichinchae***
		'Lesser' form	'Southern' form	
Body size	Larger to smaller	Smaller	Larger	Larger
Coloration	Greyer	Darker	Greyer	Darker
Abdominal band	Complete	Complete	Incomplete	Incomplete
Tail-bands	Broader	Narrower	Broader	Narrower

(1936) description of *F. f. septentrionalis* as having a 'brownish shade' and *F. f. femoralis* as 'more bluish slate' than *F. f. septentrionalis*.

That the descriptions of plumage are idiosyncratic is obviously just one of several reasons to question the validity (and utility) of these subspecies. In particular, the initial diagnoses depended on unacceptably small sample sizes of specimens (two for *F. f. septentrionalis*, three for *F. f. pichinchae*), inaccurate initial impressions of breeding status and migratory behaviour, and of course lack of genetic or statistical analyses. Another concern is that the diagnostic characters are not consistent geographically (Wilson & Brown 1953, Barrowclough 1982). Incomplete abdominal bands occur in *F. f. pichinchae* and southernmost *F. f. femoralis*; pale greyish upperparts in *F. f. septentrionalis* and southernmost *F. f. femoralis*; darker or at least less pale coloration in *F. f. pichinchae* and tropical *F. f. femoralis*; broader white tail-bands in *F. f. septentrionalis* and southern *F. f. femoralis*; and larger body size occurs in northernmost *F. f. septentrionalis*, *F. f. pichinchae* and southernmost *F. f. femoralis* (Tables 2–3).

Such deficiencies indicate that these subspecies should be re-evaluated using modern tests of diagnosability (Amadon 1949, Patten & Unitt 2002, Dickinson & Remsen 2013, Patten 2015, Patten & Remsen 2017). This requires evidence that for each quantifiable diagnostic trait at least 75% of the measurements of one subspecies overlap with no more than 1% of those of another subspecies, and vice versa (Amadon 1949, Patten & Unitt 2002, Baker *et al*. 2002). This test, in effect, determines whether diagnostic characters vary discontinuously (non-clinally) across some pre-established boundary (Huxley 1939, James 1970, 2010, Patten 2010). This re-evaluation is already in progress via an examination of geographic variation in size, proportions and plumage of specimens and live birds. Future work should also characterise the genetic basis for this variation.

Complicating any modern re-evaluation is the possibility that climate change, habitat modification and large-scale reintroduction efforts have altered or eliminated any regions of non-clinal variation that may have formerly constituted valid boundaries between

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subspecies. This implies that any re-analysis based on measurements of older specimens may no longer reflect current patterns of geographic variation. Likewise, any re-analysis and generalisations (including my own) based on more recent distribution records and morphological variation may no longer be relevant to patterns present in late 19th and early 20th century specimens. Several studies have documented recent and rapid changes in avian body size—usually decreases—associated with rising global temperatures (Johnston & Selander 1964, Tornberg *et al*. 1999, Root *et al*. 2003, Root & Schneider 2006, Parmesan 2006, Yom-Tov & Yom-Tov 2006, Hitch & Leberg 2007, Sorte & Thompson 2007, Teplitsky *et al*. 2008, Gardner *et al*. 2009, Popy *et al*. 2010, Van Buskirk *et al*. 2010, Chen *et al*. 2011, Gardner *et al*. 2011, Matthews *et al*. 2011, Kirchman & Schneider 2014). Much of this shift is probably related to the influence of climatic regimes (temperature and humidity) on body size because the latter determines rates of heat loss or gain (Bergmann 1847, James 1970, 1991). This suggests that rising global temperatures have reduced the advantage of being large (for better heat conservation) in seasonally cooler climates and increased the advantage of being small (for better heat dissipation) in hotter, more humid environments (James 1970). This is obviously relevant to Aplomado Falcon because body size is or was the most important character used to diagnose subspecies. Diagnosability, as the degree of overlap in body size or any other character, depends on the degree to which subspecies disperse and interbreed at putative boundaries, and this depends on the extent to which climate regimes and habitat fragmentation have inhibited or promoted gene flow along latitudinal and elevational gradients.

Recent climate change and habitat disturbance have probably influenced geographic variation and the extent of interbreeding by Aplomado Falcons at potential subspecies boundaries by determining the spacing and extent of suitable grassland-savanna habitat. Deforestation has reversed a climate-driven trend toward expansion of tropical forest that began in the late Holocene (see review by Werneck 2011). In this regard, conversion of tropical forest to pasture has increased availability and contiguity of habitat in the tropical lowlands (Dirzo & Garcia 1992, Estrada *et al*. 1997, Achard *et al*. 2002, De Labra *et al*. 2013). This is especially evident on the Caribbean slope of Mexico where the species has clearly benefitted from removal and thinning of tropical deciduous and evergreen forests (Keddy-Hector *et al*. 2014, 2017). Deforestation may also account for its increasing presence in Guatemala (Eisermann & Avendaño 2018) and perhaps other parts of Central America.

In the subtropical to temperate grasslands of the Chihuahuan Desert and coastal prairies of southern Texas and north-east Mexico, climate change has probably reduced available habitat by promoting conversion of desert (or 'semi-desert') grasslands to shrubland or chaparral during the past two centuries (Buffington & Herbel 1965, Powell 1994). Exacerbating climate influences has been overgrazing by livestock and the expansion of dry-land farming. This has eliminated much desert grassland and promoted the rapid decline and near-extirpation of Chihuahuan Desert Aplomado populations studied by Montoya (1995), Macías-Duarte (2002) and Macías-Duarte *et al*. (2016). Prolonged drought has contributed to this decline by reducing prey availability and, in turn, falcon productivity (Macías-Duarte *et al*. 2004, 2016).

Large-scale translocation of Aplomado Falcons has the same potential as climate change and habitat alteration to blur or eliminate subspecies boundaries via increased gene flow (Storfer 1999, Avise 2004, Williford *et al*. 2014). This is particularly relevant to *F. f. septentrionalis* because, during 1985–2013, 1,893 captive-reared southern Mexican Aplomado Falcons were released in Texas and New Mexico. A surviving population of *c*.40 resident pairs in southern Texas is now managed to maximise productivity (Hunt *et al*. 2013). Many of these birds were released in close proximity to extant populations in Chihuahua and

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southern New Mexico. Given uncertainty as to the validity of *F. f. septentrionalis* and the current southernmost extent of its distribution, it is possible that falcons released into the USA were more similar, in genetic, phenotypic and ecological terms to tropical lowland *F. f. femoralis* of Central America and northern South America than to the larger, upland, desert grassland-inhabiting *F. f. septentrionalis*. This was addressed preliminarily by Fleischer *et al*. (1998) who compared mtDNA and microsatellite DNA from Chihuahuan Desert falcons with captive southern Mexican individuals. Although this analysis found little difference between the two populations, the authors cautioned that their methodology was perhaps inadequate to detect some differences. The study also did not analyse mtDNA or microsatellite DNA from nearby putative *F. f. femoralis* populations. Ball *et al*. (1988), Winker (2009), Pérez-Emán *et al*. (2010), Oyler-McCance *et al*. (2010), James (2010), Patten (2015), Patten & Remsen (2017) and others have noted the limitations of neutral genetic markers like mtDNA to detect divergence in heritable variation of locally adaptive phenotypes.

These realities raise a concern as to the effect of this type of translocation, via releases of progeny of tropical lowland Aplomado Falcons, on declining populations in northern Mexico (Cunningham 1996, Snyder *et al*. 1996, Araki *et al*. 2007, Fraser 2008, Griffiths & Pavajeau 2008, Jacobsen *et al*. 2008, Leberg & Firmin 2008, Robert 2009). Introductions and translocations have the potential to dilute alleles responsible for adaptive phenotypic features and disrupt culturally transmitted adaptive behaviours, but might also provide long-term benefits by increasing genetic diversity and the evolutionary potential of target populations (Tallmon *et al*. 2004, Whiteley *et al*. 2014). They may also be controversial from a legal standpoint if such efforts flood populations of listed subspecies with genotypes of unlisted races.

The potential for detrimental impacts to declining Chihuahuan Desert populations is troubling, mainly because the larger size and desert to semi-desert habitat of these birds sets them apart both phenotypically and ecologically from lower elevation Aplomado Falcons that now range more or less continuously from southern Texas to South America. This distinctiveness was the basis for Todd's (1916) diagnosis of *F. f. septentrionalis*. Responsible action requires careful consideration of the potential impacts of such introductions before flooding this region with descendants of smaller tropical lowland falcons. The primary objective, as a means to preserve evolutionary potential and viable metapopulation structure, should be to preserve this desert-grassland, higher elevation form and its gene pool. One way to achieve this is to provide legal protection for the Chihuahuan Desert or Mexican Altiplano Aplomado Falcon as a 'distinct population segment' as provided for under the US Endangered Species Act (Haig *et al*. 2006, Haig & Delia 2010). Such protection would sharpen the focus of conservation actions on a region where Aplomado Falcons are actually in trouble, and away from the Gulf coast of Texas and Caribbean slope of Mexico where no recent declines have been reported and the species appears relatively secure (Keddy-Hector *et al*. 2017).

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